PHYLOGENETIC RELATIONSHIPS OF ELEOTRIDID FISHES (PERCIFORMES: GOBIOIDEI)

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ABSTRACT

Several features that have been used to classify gobioid fishes are discussed. Polarity information is provided, when evidence is available, to provide better information for further studies on gobioid relationships. Odontobutidae new family is described to include three genera (*Micropercops, Odontobutis* and *Perccottus*) that had been previously assigned to the Eleotrididae. Four synapomorphies associated with the pectoral girdle, caudal skeleton, dorsal fin, and scale morphology corroborate monophyly of a group consisting of all gobioids except odontobutids and rhyacichthyids. The remaining eleotridids are assigned to the gobiid subfamilies Butinae and Eleotridinae. Specializations in the jaw musculature and caudal skeleton are presented to define the subfamily Eleotridinae. Patterns of papilla and pterygiophore insertion are congruent within the odontobutids and butines, but show little congruence within the Eleotridinae, and we conclude that while these characters may be of some value in investigating relationships within families and subfamilies, they are uninformative of interfamilial relationships within the Gobioidei.

The Gobioidei is one of the largest vertebrate suborders with approximately 2,000 extant species of freshwater, estuarine, and marine fishes classified in about 270 genera. This high diversity, coupled with the small adult size of most species, has contributed to a poor understanding of the taxonomy of the group, and the classification of gobioids has been chaotic. Our poor understanding of gobioid phylogeny can largely be attributed to the absence of a well-corroborated sister group hypothesis for the suborder, a scarcity of cladistic studies to hypothesize relationships, the small number of characters surveyed, and the reductive and often highly labile nature of the specializations identified.

Birdsong (1975) attempted to define generalized and specialized character states based largely on transitional series within the group. More recently, Springer (1983, 1988) defined gobioid specializations by using all other perciforms as an outgroup. Hoese (1984) presented a classification of gobioid fishes based on the same assumptions as Springer (1983). Akihito (1986) provided polarity information using seven perciform families as outgroups.

There is some consensus in recent classifications of gobioid fishes. Most importantly, the Rhyacichthyidae, containing only *Rhyacichthys aspro* (Valenciennes), has been corroborated as the sister group of all other gobioids. However, Akihito (1986) suggested that *Rhyacichthys* might not be close to a gobioid ancestor, because of its specializations for torrential streams. Evidence for the Rhyacichthyidae forming the sister group to all other gobioids includes three unequivocal synapomorphies for all other gobioids: lateral line canal not extending onto the body; ventral process of the hyomandibula broad with the dorsal tips of the interhyal and symplectic widely separated from each other; and mandibular sensory canal absent (Springer, 1983). To this list we add two synapomorphies, change in the position of the penultimate branchiostegal ray (see below) and reduction of head canals (separation of preopercular canal from oculoscapular canal and possibly reduction in number of pores).

The extant non-rhyacichthyid gobioids have been variously placed in one (Miller, 1973; Akihito, 1986) to five families (Hoese, 1984; Birdsong et al., 1988). These families are generally divided into two groups: one for species with 6

branchiostegal rays (i.e., Eleotridinae of Akihito, 1986; Eleotrididae and Xenisthmidae of Hoese, 1984) and one for species with 5 branchiostegal rays (i.e., Gobiinae of Akihito, 1986; Gobiidae, Kraemeriidae and Microdesmidae of Hoese, 1984). Six branchiostegal rays is plesiomorphic within the Gobioidei (generalized perciforms have 6 or 7), and the loss of one ray may be a synapomorphy for the group with 5 rays. Of the six-branchiostegal-rayed taxa, the Xenisthmidae are well diagnosed by at least four synapomorphies (Springer, 1983, 1988; Gill and Hoese, in prep.). One major question remaining is whether the other six-branchiostegal-rayed group, the Eleotrididae, is monophyletic, or whether some of its taxa are more closely related to other gobioid families than they are to the remaining eleotridids. This question prompted our study of eleotridid relationships. Herein we discuss several characters that may be informative in the higher classification of gobioids, and provide evidence for the monophyly of some groups.

Regan (1911) was the first to use osteological features for the classification of gobioid fishes. Gosline (1955) added microdesmids and kraemeriids to the gobioids based on osteological attributes. More recently Miller (1973) produced a considerably different classification based largely on osteological characters and reviewed much of the earlier literature on gobioid classification. Miller's classification was criticized by Birdsong (1975) largely for the limited number of taxa examined and the inability to establish homologies for many characters. Springer (1983) noted errors in Miller's osteology, and excluded the Pholidichthyidae, which Miller had included among the gobioids. Springer (1983) provided information on specializations defining xenisthmids and separating other gobioid fishes from *Rhyacichthys*. He was the first to apply cladistic methods.

Considerable importance has been placed in recent years on two gobioid characters: the pattern of sensory papillae and the arrangement of pterygiophores of the first dorsal fin. Although these characters are useful for identification of species and genera, their use in determining phylogenetic relationships is suspect because of difficulty in hypothesizing homology and polarity of various character states. Hoese (1983) showed that in some cases the papillary patterns can be polarized based on ontogeny, but evidence was also presented for convergence in two unrelated genera. The papillary and pterygiophore patterns, however, do show some degree of congruence with other characters, as discussed below.

Although some studies (Birdsong, 1975; Birdsong et al., 1988; Harrison, 1989; Springer, 1983) have identified potentially informative variation in some osteological structures, none of the existing classifications has been based on surveys of large number of characters in a large number of genera.

Many studies have been based on a relatively general investigation of the osteology of one or a few species at most (TeWinkel, 1935; Lele and Kulkarni, 1938, 1939; Miller, 1963; Dornesco and Misculenco, 1968; Birdsong, 1975; Miller and Wongrat, 1979; Winterbottom and Emery, 1981; Murdy, 1985; Vasil'yeva, 1984, 1989; Van Tassell et al., 1988; Winterbottom and Burridge, 1989; Winterbottom, 1990). Other studies have concentrated on the osteology of larger groups, such as smaller families and subfamilies (Gosline, 1955; Miller, 1973; Springer, 1983, 1988; Rennis and Hoese, 1987; Murdy, 1989). Still other studies have concentrated on surveys of few characters throughout a broad number of genera (Akihito, 1963, 1967, 1969, 1971, 1986; Birdsong et al., 1988). Our study falls into this last category.

We recognize three groups previously included in the family Eleotrididae: the Odontobutidae (new family) including three genera (*Micropercops* Fowler and Bean, *Odontobutis* Bleeker, and *Perccottus* Dybowski), the gobiid subfamily Butinae including 13 genera (Table 1), and the gobiid subfamily Eleotridinae in-

cluding 21 genera (Table 2). We diagnose the last subfamily by the synapomorphies of the adductor mandibulae tendon attachment to the maxilla and posterior prolongation of the procurrent caudal cartilages (see below).

Materials and Methods

Osteological studies were made from trypsin digested material stained for bone with alizarin red-S (following Taylor, 1967). Some material was also counterstained for cartilage with alcian blue, following the method of Taylor and Van Dyke (1985). Dissection of cleared and stained specimens follows Weitzman (1974). Cartilage was also examined in non-alcian blue stained material using dark field illumination with a Zeiss SV-8 dissecting microscope. Some osteological details in specimens unavailable for clearing and staining were determined from radiographs. Jaw musculature and tendon attachments were studied from cleared and stained material and from dissections of preserved specimens. Muscle terminology follows Winterbottom (1974). Some caudal-fin ray counts were made from radiographs and from specimens examined with transmitted light. Characters were polarized by outgroup comparison with *Rhyacichthys* and a diverse range of perciforms and other acanthomorph fishes; a detailed record of these materials was not maintained.

Osteological Material Examined. —Institutional abbreviations follow Leviton et al. (1985); numbers of specimens examined are followed in parentheses by mm standard length ranges.

GOBIIDAE: BUTINAE. *Bostrychus sinensis*—CAS-SU 24226, 1 (65). *Butis amboinensis*—AMS I.27265-001, 1 (74); USNM 224964, 2 (36–47). *Butis butis*—AMS I.16670-028, 3 (48–74). *Hannoichthys africanus*—CAS-SU 40431, 1 (65). *Incara multisquamatus*—AMS I.22720-023, 2 (30–32); AMS I.23279-012, 2 (31–40). *Kribia kribensis*—CAS-SU 40432, 1 (36). *Kribia elongata*—CAS-SU 64538, 3 (19–20). *Milyeringa veritas*—AMS I.21336-001, 4 (31–43). *Ophiocara porocephala*—AMS I.22709-010, 1 (44). *Oxyeleotris aruensis*—AMS I.16813-002, 1 (46). *Oxyeleotris lineolata*—AMS I.16835-008, 1 (19); AMS I.20848-021, 15 (23–90). *Oxyeleotris nullipora*—AMS I.21237-010, 20 (14–27); AMS I.23296-012, 3 (25–36); AMS I.21239-007, 3 (17–28). *Prionobutis microps*—AMS I.18501-002, 1 (47); AMS I.25520-001, 1 (45); AMS I.23287-017, 1 (35). *Typhleotris madagascariensis*—MNHN 1949-12, 2 (radiographs).

GOBIIDAE: ELEOTRIDINAE. *Bunaka gyrinoides*—AMS I.31518-001, 1 (74). *Calumia godeffroyi*—AMS I.19480-026, 1 (18); USNM 224966, 1 (23). *Calumia profunda*—AMS I.21918-068, 1 (14). *Dormitator maculatus*—SIO H46-253, 2 (57–63). *Eleotris melanosoma*—AMS I.22709-009, 3 (25–54). *Eleotris sandwichensis*—AMS I.27266-001, 3 (32–42). *Erotelis armiger*—UCLA W57-41, 1 (37); AMS I.27267-001, 1 (50). *Erotelis smaragdus*—AMS I.27268-001, 1 (45). *Gobiomorphus australis*—AMS I.18940-010, 10 (20–65); AMS I.27254-001, 2 (30–32); AMS I.27255-001, 1 (56). *Gobiomorphus breviceps*—AMS I.27269-001, 2 (61–74). *Gobiomorphus cotidianus*—AMS I.27269-002, 2 (54–72); AMS I.27269-003, 1 (64). *Gobiomorphus coxii*—AMS I.15335-008, 6 (48–59); AMS I.27254-002, 1 (65); AMS I.27270-001, 1 (98). *Gobiomorphus hubbsi*—AMS I.27269-004, 2 (43–52). *Gobiomorus maculatus*—SIO 62-46, 1 (57). *Grahamichthys radiatus*—AMS I.27271-001, 2 (41–47); AMS I.27272-001, 1 (43). *Guavina guavina*—USNM 79083, 1 (134) (radiograph). *Hemieleotris latifasciatus*—LACM 4787, 2 (46–46). *Hypseleotris guntheri*—UCLA W65-29, 2 (44–53). *Hypseleotris* sp. 4—AMS I.18965-009, 4 (32–46); AMS I.25257-002, 9 (27–35); AMS I.21284-005, 5 (19–24). *Hypseleotris* sp. 5—AMS I.25257-003, 5 (29–37); AMS I.25257-004, 6 (30–37). *Hypseleotris aurea*—AMS I.25492-005, 4 (24–28). *Hypseleotris compressa*—AMS I.22088-003, 7 (28–41); AMS I.22699-004, 3 (18–23); AMS I.22710-004, 6 (16–38). *Hypseleotris galii*—AMS I.27273-001, 10 (22–36). *Hypseleotris klunzingeri*—AMS I.17616-001, 6 (28–37); AMS I.25257-001, 4 (25–38). *Hypseleotris regalis*—AMS I.22744-002, 1 (31). *Kimberleyeleotris hutchinsi*—WAM P.25864-007, 2 (27–24). *Leptophilypnus* sp.—AMS I.31522-001, 1 (31). *Leptophilypnus fluviatilis*—AMS I.27274-001, 2 (27–28). *Microphilypnus* sp.—AMS I.31523-001, 3 (10–16). *Mogurnda adspersa*—AMS I.22096-007, 1 (50). *Mogurnda mogurnda*—AMS I.27276-001, 8 (25–68). *Mogurnda nesolepis*—WAM P.27848-001, 6 (16–31). *Mogurnda* sp.—WAM P.26979-003, 1 (37). *Ophieleotris aporos*—AMS I.22710-005, 3 (28–31). *Philypnodon grandiceps*—AMS I.17618-007, 10 (46–60); AMS I.27256-001, 2 (40–42). *Philypnodon* sp.—AMS I.20111-003, 3 (28–36); AMS I.20111-004, 4 (39–40); AMS I.27252-001, 4 (30–35). *Ratsirakea legendrei*—AMS I.31521-001, 1 (42). *Tateurndina ocellicauda*—AMS I.27280-001, 2 (26–28). *Thalasseleotris adela*—AMS I.18241-035, 6 (20–27).

GOBIIDAE: GOBIINAE. *Acentrogobius viridipunctatus*—AMS I.22720-010, 2 (36–50); AMS I.23265-001, 4 (33–60). *Acentrogobius janthinopterus*—AMS I.20978-014, 2 (27–66); AMS I.22724, 1 (41). *Awaous crassilabrus*—AMS I.23296-002, 1 (59). *Bathygobius laddi*—AMS I.23365-002, 6 (24–34). *Boleophthalmus birdsongi*—AMS I.22789, 1 (50). *Boleophthalmus boddarti*—AMS I.21030-006, 2 (88–91). *Brachyamblyopus olivaceous*—CAS-SU 38460, 2 (35–54). *Chaenogobius macrognathus*—CAS-SU 6585, 1 (35). *Chlamydogobius eremius*—AMS I.13661, 1 (37). *Glossogobius circumspectus*—AMS I.22720, 1 (49). *Glossogobius concavifrons*—AMS I.23269-001, 2 (26–31). *Glossogobius aureus*—

AMS I.22080-001, 5 (35–44). *Gnatholepis thompsoni*—SIO 65-539, 2 (24–39). *Hemigobius crassa*—CAS-SU 38636, 1 (28). *Lepidogobius lepidus*—SIO H51-242, 1 (43). *Mugilogobius* sp.—AMS I.22699, 4 (13–21). *Nesogobius pulchellus*—AMS I.16799-025, 2 (28–31). *Oxyurichthys tentacularis*—AMS I.21901-003, 2 (67–76). *Pseudogobius* sp.—AMS I.22720-003, 7 (16–31). *Redigobius balteatus*—AMS I.22700, 3 (20–25); AMS I.22709, 1 (23). *Redigobius chrysosoma*—AMS I.22699, 1 (18). *Redigobius macrostoma*—AMS I.31525-001, 6 (24–32). *Rhinogobius brunneus*—AMS I.31524-001, 2 (18–42). *Rhinogobius mekongianus*—AMS I.25973-001, 1 (31). *Sicydium cocoensis*—SIO 59-333, 2 (37). *Stenogobius genivittatus*—SIO 61-425, 1 (54). *Tamanka siitensis*—AMS I.19194-001, 2 (41–44). *Taenioides purpurascens*—AMS I.19836-001, 1 (108). *Tridentiger trigonocephalus*—SIO 63-1059, 1 (41).

KRAEMERIIDAE. *Kraemeria* sp.—AMS I.22724, 2 (32–33). *Kraemeria bryani*—USNM 143153, 2 (15–20).

MICRODESMIDAE: MICRODESMINAE. *Cerdale ionthas*—AMS I.24368-001, 1 (57). *Gunnellichthys monostigma*—AMS I.17489-001, 1 (53).

MICRODESMIDAE: PTERELEOTRINAE. *Aioliops tetrophthalmus*—AMS I.22581-037, 2 (17–19). *Aioliops megastigma*—AMS I.25435-001, 2 (16–18). *Nemateleotris magnificus*—AMS I.17027-001, 1 (32). *Nemateleotris decora*—AMS I.19476-045, 1 (50). *Parioglossus formosus*—AMS IA.769, 1 (24). *Parioglossus palustris*—AMS I.22849-002, 2 (23–34). *Parioglossus formosus*—AMS IA.769, 2 (28–30). *Ptereleotris evides*—AMS I.15643-014, 2 (51–53). *Ptereleotris monoptera*—AMS I.15678-007, 1 (70). *Ptereleotris zebra*—AMS I.15621-012, 4 (51–74).

ODONTOBUTIDAE. *Micropercops swinhonis*—AMS I.27275-001, 2 (42). *Odontobutis obscura*—AMS I.27277-001, 2 (42–68). *Perccottus glehni*—USNM 105188, 1 (63) (radiograph).

RHYACICHTHYIDAE. *Rhyacichthys aspro*—AMNH 48695, 1 (103); CAS-SU 38565, 1 (116); USNM 247300, 1 (167) (superficial bones of head, and branchial and hyoid arches only).

XENISTHMIDAE. New gen. and sp.—AMS I.32484-001, 1 (31). *Rotuma lewisi*—USNM 280289, 1 (18). *Tyson belos*—USNM 229985, 1 (19). *Xenisthmus* sp.—USNM 247387, 1 (25). *Xenisthmus africanus*—ROM CS51482, 2 (25). *Xenisthmus polyzonatus*—AMS I.22579-062, 1 (19).

In addition, external morphology was examined on numerous specimens of various species housed in collections in the Australian Museum and the Smithsonian Institution and on types of gobioid fishes in various museums.

CHARACTER DESCRIPTIONS AND POLARITIES

Fourteen characters used in the analysis were studied for which polarity information is provided. These characters include: 1) attachment of adductor mandibulae tendon; 2) anterior development of procurrent caudal cartilages; 3) posterior development of procurrent caudal cartilages; 4) scapula development; 5) presence of autogenous middle radial of first pterygiophore of second dorsal fin; 6) development of bony preopercular canal support; 7) scale cteni morphology; 8) position of penultimate branchiostegal ray; 9) preopercular-mandibular head canal development; 10) lateral line development; 11) infraorbital canal development; 12) urohyal shelf; 13) interneural gap; and 14) interhyal position. Two specializations for gobiines are taken from Hoese (1984): 15) branchiostegal-ray number and 16) pelvic fins. Also polarity information is provided for the following five characters. These were not used in the analysis because of the high variability within a genus and/or species, or because we believe the characters not to be truly independent of other characters used: 1a) separation of A1-beta segment of adductor mandibulae muscle; 2a) number of caudal rays; 3a) number of epurals; 4a) scapula ossification; and 5a) head pore development. Two additional characters for which we were unable to provide polarity information were also studied: pattern of sensory papillae and pterygiophore formula. Discussions of these two characters are included because they have been suggested by other workers to be important in goby classification (Miller et al., 1989; Birdsong et al., 1988).

Attachment of Adductor Mandibulae Tendon and Jaw Musculature.—In most perciform and other acanthomorph fishes the adductor mandibulae tendon (character 1) attaches just posterior to or on the head of the maxilla, and we regard this as the primitive condition. We assume here that the adductor mandibulae tendon in gobioids is homologous with that of perciforms. In *Rhyacichthys* the

tendon inserts on the posterodorsolateral margin of the maxilla (R. Winterbottom, in litt.). The forward position of the mouth in *Rhyacichthys* is regarded here as a *Rhyacichthys* specialization in relation to perciforms and we regard the tendon attachment in *Rhyacichthys* as derived. In odontobutids and butines the adductor mandibulae tendon attaches anteriorly on the inner side of the maxilla just posterior to the maxillary head (Fig. 1A). In all species studied in these groups the tendon attaches to a short process extending from the maxilla. The maxillodentary (=primordial) ligament attaches to the lateral side of the maxilla about halfway down its shaft. In cleared and stained material it was often not possible to separate the ligament from the tendon of the main adductor mandibulae muscle mass, because the two are close together and the element labelled ligament in Figure 1 may in some cases actually be a tendon. Because the variation noted was only in the upper tendon, that distinction does not affect the following discussion. Eleotridines are more derived than odontobutids and butines in having the tendon attached medially about halfway down the maxilla shaft, usually posterior to the attachment of the maxillodentary ligament, except in *Grahamichthys* and *Thalasseleotris* (the attachment is only slightly anterior to the maxillodentary ligament attachment). The tendon attaches directly to the shaft (Fig. 1B), often in a groove or depression, and there is never a process extending from the maxilla.

In some putatively primitive gobiine genera examined (*Redigobius* and *Pseudogobius*) the tendon attachment of the adductor mandibulae is similar to that of butines and odontobutids. The other gobiines examined exhibited a range of attachment types; in some species there were two attachments, while in others there was a broad attachment with the tendon reduced to a thin segment along the maxilla shaft. Further studies of the jaw musculature of gobiines may help to resolve relationships within the family, given the number of different patterns observed.

In butine and odontobutid genera there is a distinct A1-beta segment of the adductor mandibulae muscle separate from the main muscle mass, running beneath the eye. In the dwarf *Oxyeleotris nullipora* there is a single muscle mass without a separate A1-beta segment. In *Rhyacichthys* the A1-beta segment is not distinguishable. Similarly perciforms and other acanthomorphs do not usually have an A1-beta segment. Consequently the separation of this muscle mass may be a specialization for the Butinae and the Odontobutidae (assuming a reversal in *Oxyeleotris nullipora*). The A1-beta segment is not separate from the main muscle mass in eleotridines and most other gobioids examined (except in the gobiines *Pseudogobius* and *Redigobius*). This character was not used in the final analysis because it may not be independent of the tendon attachment.

Caudal Skeleton. —For the discussion that follows we treat four characters in the caudal skeleton: number of rays, number of epurals, anterior development of the dorsal and ventral procurrent cartilages (character 2), and the posterior development of the cartilages (character 3). However, as discussed below, we believe that the number of segmented rays and the posterior procurrent caudal cartilage development are probably linked. In most gobioid fishes there are 17 segmented caudal rays and usually four or more unsegmented rays dorsally and four or more ventrally. We use the term unsegmented rather than procurrent caudal-fin rays, because procurrent rays are usually defined as those dorsal and ventral to the principal caudal rays, which are often defined to include the branched rays plus the unbranched ray immediately above and below the branched rays (Hubbs and Lagler, 1958). We also avoid the term procurrent for the unsegmented rays in gobioids because the number of branched rays is highly variable (0–17) and often
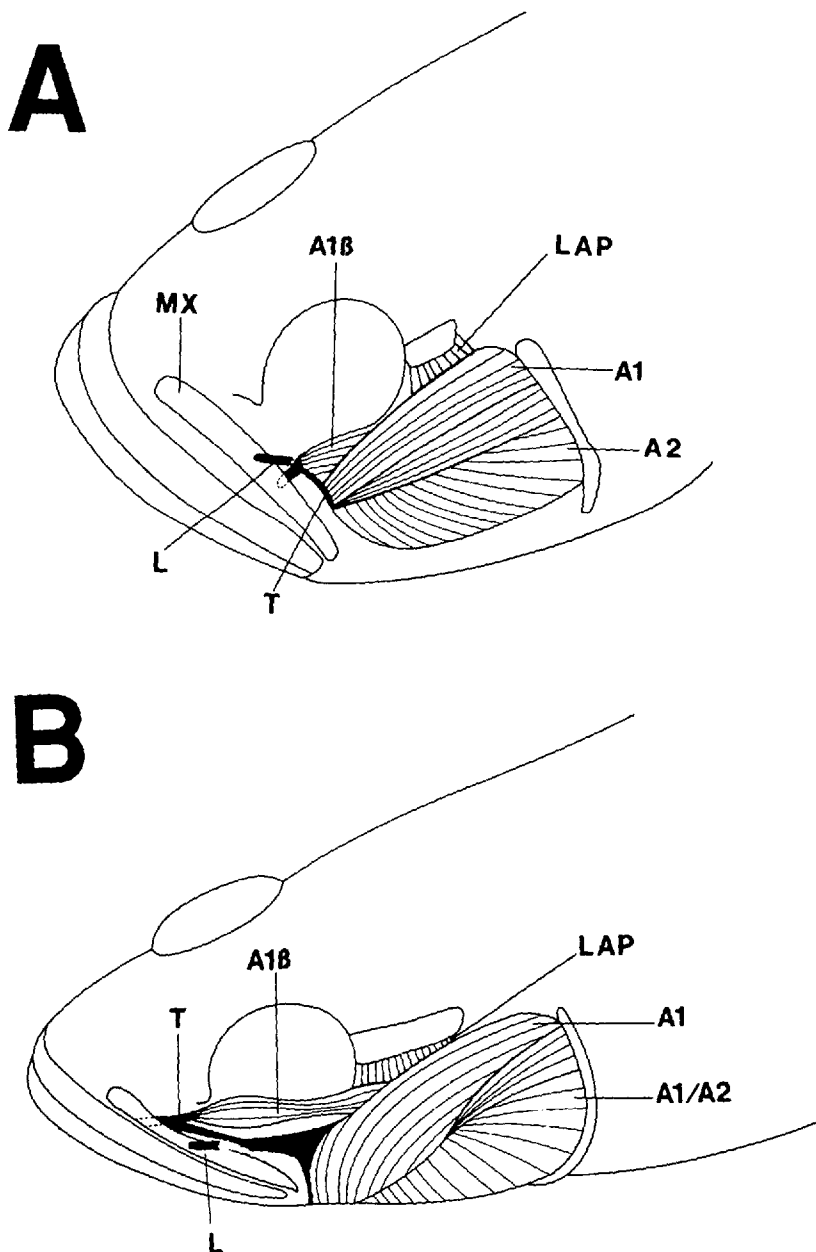
Figure 1.   Jaw musculature of: A) *Oxyeleotris lineolata*, AMS I.16835-008 and AMS I.20848-021, based on several specimens; B) *Eleotris melanosoma*, AMS I.22041-003, based on several specimens. Abbreviations: MX—maxilla; A1 beta, A1 and A2—segments of adductor mandibulae muscle; LAP—levator arcus palatini; T—adductor mandibulae tendon; L—maxillo-dentary ligament (only partly shown).

increases with increasing size within a given species. The segmented caudal rays in gobioid fishes normally articulate as follows (dorsal to ventral): the uppermost ray is associated with the epural (when only one epural is present) or posterior epural (when two or three epurals are present), the next with hypural 5, the next

seven with the upper hypural plate (hypurals 3+4), the next six with the ventral hypural plate (hypurals 1+2), the next one with the parhypural, and the lowermost with the expanded hemal spine of the penultimate vertebra (pu2). Some displacement occurs and a ray may overlap two bones. The unsegmented caudal rays articulate with large cartilage plates (one dorsal and one ventral) and sometimes with epurals.

Anterior Extent of Procurrent Cartilages (character 2).—Odontobutids resemble rhyacichthyids (and generalized perciforms) and differ from other gobioids in having relatively small dorsal and ventral procurrent cartilages that do not extend anteriorly to support the anterior unsegmented rays (Fig. 2A). We consider the anterior expansion of the procurrent cartilages to be derived within the Gobioidei, and thus providing evidence for monophyly of all gobioids, exclusive of odontobutids and rhyacichthyids.

Posterior Extent of Procurrent Cartilages (character 3).—In butines, odontobutids, and gobiines the upper procurrent cartilage plate is relatively short posteriorly, not extending over the tip of the epural or epurals (Fig. 2B). It may extend over the tip of the anteriormost epural in some gobiines (Fig. 2C). In some specimens there may be a detached block of cartilage above the epural.

In eleotridines the procurrent cartilages are posteriorly (and anteriorly) elongate. The dorsal procurrent cartilage typically has a thin elongate extension over the tip of the epural(s) (Fig. 2E). A similar condition exists ventrally, although the cartilage below the tip of the pu2 hemal spine is often thin and detached from the remainder of the cartilage plate. In *Tateurndina* the dorsal cartilage is posteriorly elongate but does not extend over the epural. The epural is displaced posteriorly and hypural 5 is absent. Consequently, we believe the separation of the cartilage from the epural is secondary, resulting from loss of hypural 5 and a posterior shift of the epural(s), but have coded the character as a "?" for *Tateurndina* in the data matrix.

Rhyacichthys, odontobutids, and butine genera (except for *Kribia*) have 17 segmented caudal rays. In *Kribia,* one species has 15 segmented rays and another 14 or 15 (Fig. 2D). In these species the caudal cartilages are typical of the other butine and odontobutine genera, but rays associated with the hypural plates are reduced in number (6+5 in *K. kribensis* and 6+4–5 in *K. elongata*). In specimens of *Kribia elongata* with five rays associated with the lower hypural plate, there is no ray associated with the parhypural. The loss of rays from the hypural plate is not regarded as homologous with the transformation of the uppermost and lowermost rays in eleotridines.

In eleotridines there are typically 15 segmented caudal rays, with the rays associated with the procurrent cartilages extending over the tips of the epural and the pu2 hemal spine unsegmented (Fig. 2E). Exceptions were found in three eleotridine genera. *Tateurndina* has 17 segmented caudal rays. We believe the presence of 17 rays in *Tateurndina* is a reversal resulting, in part, from the separation of the epural(s) from the dorsal procurrent cartilage. In *Thalasseleotris* about two-thirds of the specimens examined had 16 (8+8) segmented caudal rays, and the remainder had 17. The cartilage plates are elongated and the upper plate extends slightly over the tip of the epural. *Grahamichthys* also usually has 16 segmented caudal rays. It was not possible to determine other details of the caudal skeleton in this taxon due to damage in all of the available cleared and stained material. We place the three genera with the eleotridines based on the adductor mandibulae tendon attachment.
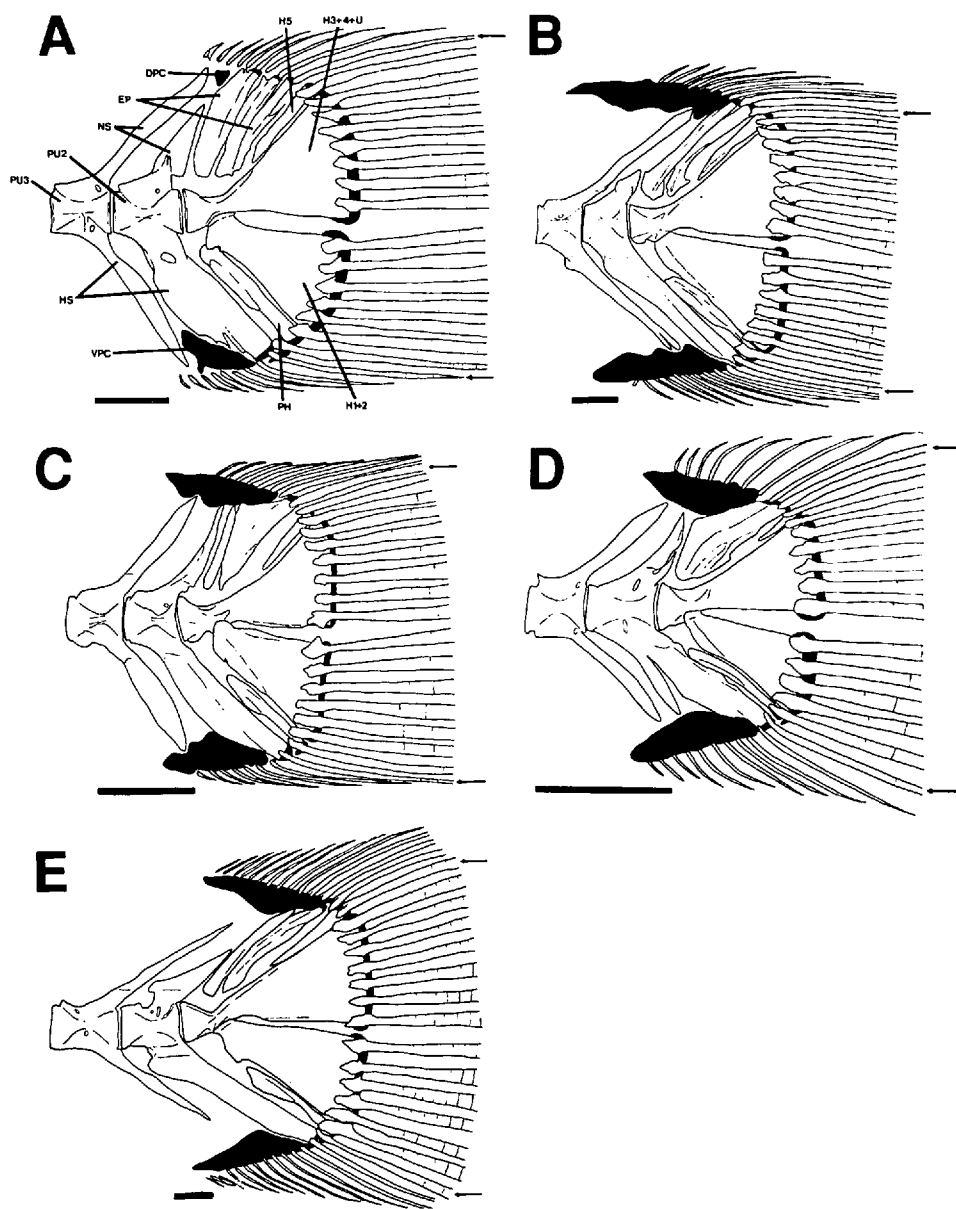
Figure 2.   Caudal skeleton of A) *Micropercops swinhonis,* AMS I.27275-002, 42 mm; B) *Ophiocara porocephala* AMS I.22709-010, 44 mm; C) *Redigobius macrostoma,* AMS I.31525-001, 26 mm; D) *Kribia elongata,* CAS-SU 64538, 20 mm SL; E) *Gobiomorus maculatus,* AMS I.30730-001, 79 mm. Abbreviations: EP—epurals; DPC—dorsal procurrent cartilage; H1+2—fused hypurals 1 and 2; H3+4+U—fused urostylar complex and hypurals 3 and 4; H5—hypural 5; HS—hemal spines; NS—neural spines; PH—parhypural; PU2-3—preural centra 2 and 3; VPC—ventral procurrent cartilage. Arrows indicate outer segmented caudal-fin rays; scale bars indicate 1 mm.

Caudal ray number was excluded from the final analysis because the condition in *Kribia* is autapomorphic and we believe the character to not be truly independent of the development of the caudal cartilage in eleotridines. It is possible that the loss of the uppermost and lowermost rays in eleotridines is related to the

procurrent cartilages each displacing a ray or preventing development of segments in the posteriormost ray associated with each cartilage.

Rhyacichthys has three epurals. Most odontobutids, butines and eleotridines have two epurals. None are known to have three epurals, except as occasional variants. One epural only occurs in *Kribia* sp., *Grahamichthys, Thalasseleotris, Ratsirakea,* some species of *Gobiomorphus,* and some specimens of *Tateurndina.* Gobiines have one or two epurals. This character was not used in further analysis because of its variation within genera and species.

Scapula Size and Position. —Akihito (1986) reported the scapula as being ossified in all eleotridines (except *Grahamichthys,* but in some genera the ossification does not enclose the foramen). We also found the scapula unossified in *Thalasseleotris.* The scapula is poorly ossified or unossified in *Microphilypnus.* Other gobioids are variable in degree of ossification and the character was not used in the final analysis.

Odontobutids and rhyacichthyids resemble generalized perciforms in having a relatively well-developed scapula (character 4) that extends dorsally to exclude contact between the upper proximal radial of the pectoral fin and the cleithrum (Fig. 3A). Other gobioids are more specialized in having the scapula reduced in size so that the radial extends dorsally past the scapula (Fig. 3B) and usually abuts the cleithrum (Fig. 3C). This character provides additional evidence of monophyly of all gobioids, exclusive of odontobutids and rhyacichthyids.

Middle Radial of First Pterygiophore of Second Dorsal Fin (character 5). —In rhyacichthyids and most specimens of odontobutids, the pterygiophore that supports the first element (primitively a spine) of the second dorsal fin is trisegmental. In some specimens of *Micropercops* an autogenous middle radial is absent. In all other gobioids we have examined the middle and proximal radials of this pterygiophore are fused (or the middle is lost?). We treat the former condition as plesiomorphic within the Gobioidei.

Bony Preopercular Canal Support (character 6). —The bony support for the preopercular canal extends most of the length of the preoperculum in rhyacichthyids, xenisthmids, odontobutids and almost all butines (Fig. 4A), even when the canal segment is reduced or absent; exceptions include at least some *Kribia* species, *Oxyeleotris nullipora,* and *O. aruensis.* In all eleotridines the canal support is confined to the vertical portion of the bone (Fig. 4B), and is often either present only dorsally or absent. With the exception of a few gobiines that have the support extending most of the length of the bone (e.g., *Redigobius* and *Gobionellus*), the canal support of other gobioids is either restricted to the vertical portion of the preoperculum or absent. We consider the restricted and absent conditions apomorphic within gobioids. The reduction of the canal support provides evidence of the monophyly of the eleotridines. Because the gobiines are well defined on other characters, we regard the reduction or loss of the canal support as convergent in some gobiines. At present we are unable to determine whether the reduced condition in some species of *Oxyeleotris* is convergent or an indication of a potential sister group of the eleotridines. The variation in *Oxyeleotris* brings into question the monophyly of that genus.

Scale Cteni (character 7). —*Rhyacichthys* has up to 11 rows of cteni on the body scales; cteni in the outer row are well developed, while those of the remaining rows are distally truncated and cuboid in shape (="transforming cteni" of Roberts, 1993; Fig. 5A). At least some body scales in odontobutids have a basal row of transforming cteni, with one or two outer rows of well-developed cteni (Fig. 5B).
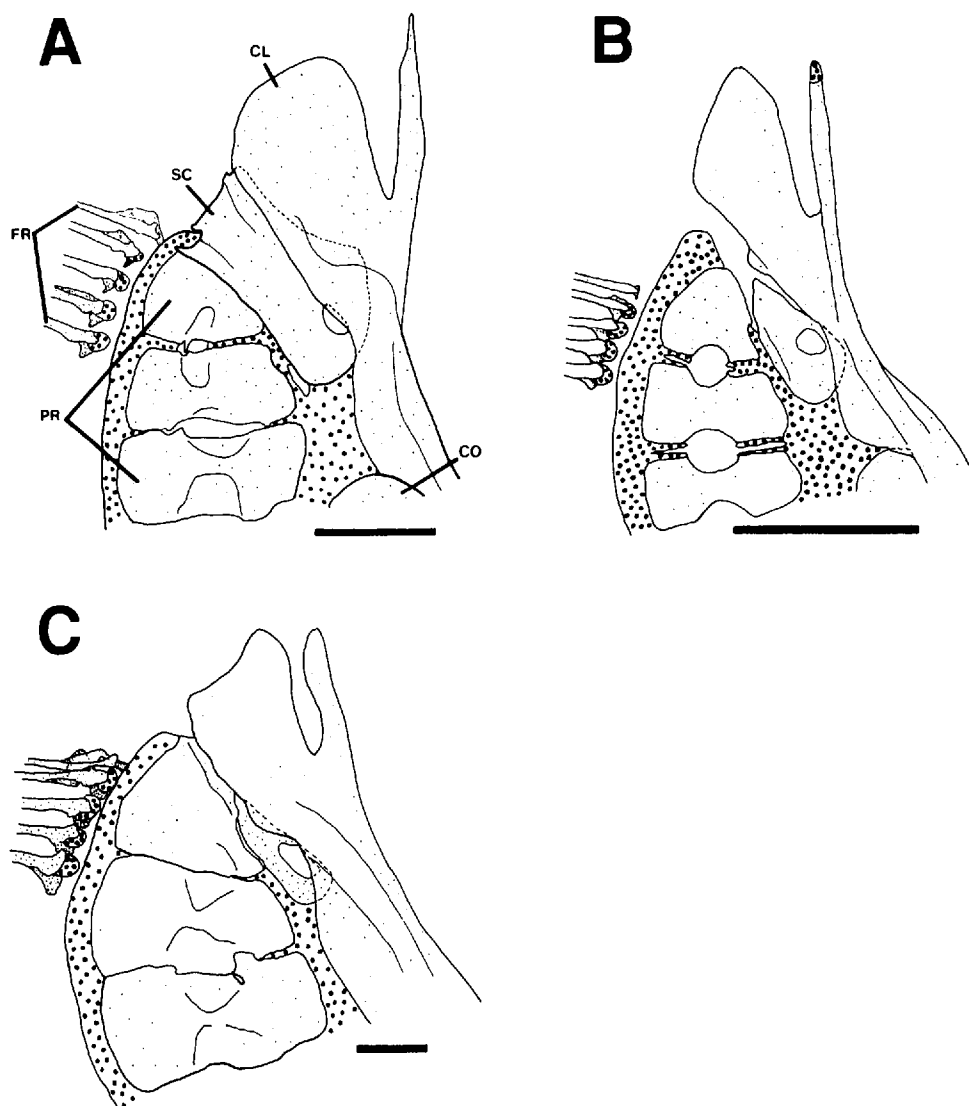
Figure 3.   Lateral views of right upper portion of cleithrum (CL), upper three proximal radials (PR), upper five fin rays (F), upper part of coracoid (CO) and scapula (SC) of: A) *Micropercops swinhonis,* AMS I.27275-002, 42 mm; B) *Hypseleotris aurea,* AMS I.25429-005, 28 mm; C) *Butis amboinensis,* AMS I.27265-001, 74 mm (coracoid not shown). Dashed lines indicate limits of bones obscured by others; scale bars indicate 1 mm.

Number of transforming cteni may be associated with size; our largest specimens of *Odontobutis* (which are larger than our largest specimens of *Micropercops* and *Perccottus*) have as many as five basal rows of transforming cteni (Fig. 5C; see also Kobayasi, 1953, fig. 11). With the exception of *Acanthogobius flavimanus,* which has a single basal row of transforming cteni (Takagi, 1953), butines, eleotridines, and other gobioids are more specialized in lacking transforming cteni on their scales (Fig. 5D).

Position of Penultimate Branchiostegal Ray (character 8).—*Rhyacichthys* resembles generalized perciforms in having two branchiostegal rays on the posterior
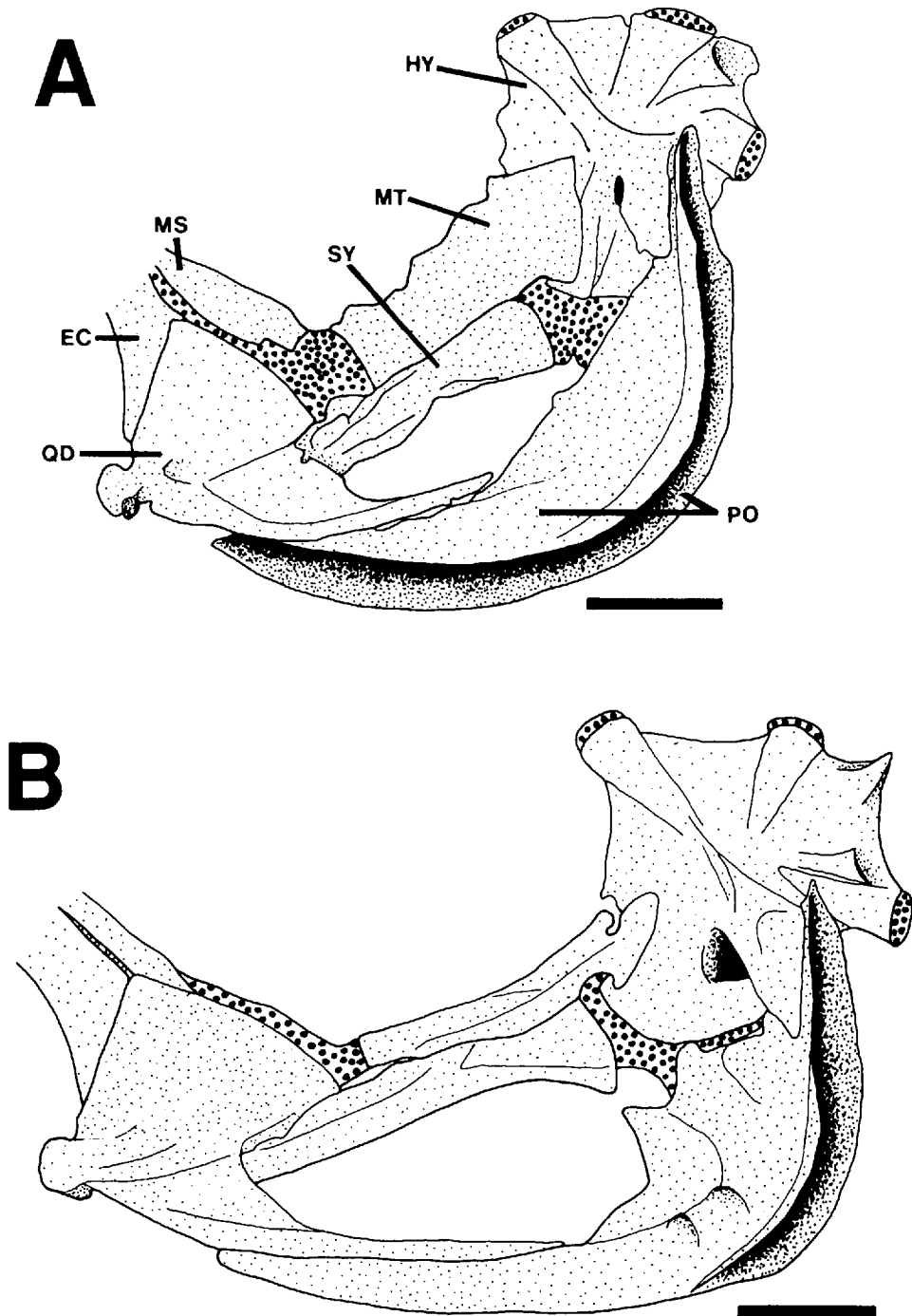
Figure 4.   Lateral views of right side (reversed) ectopterygoid (EC), hyomandibula (HY), mesopterygoid (MS), metapterygoid (MT), preoperculum (PO), quadrate (QD), and symplectic (SY) of: A) *Micropercops swinhonis,* AMS I.27275-002, 42 mm; B) *Gobiomorphus australis,* AMS I.27255-001, 56 mm. Scale bars indicate 1 mm.
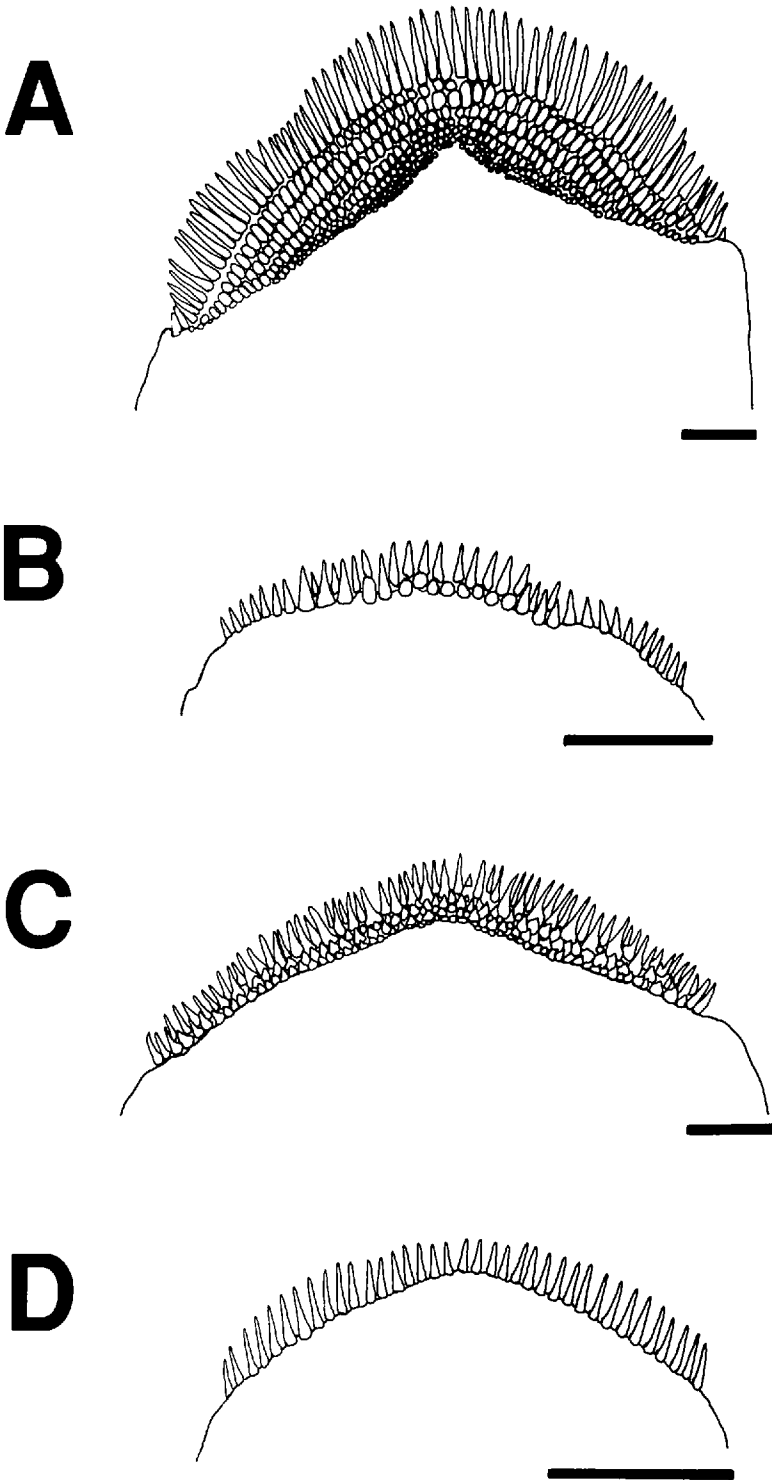
Figure 5.   Posterior margin of body scales (from several lateral rows above anal fin origin) of: A) *Rhyacichthys aspro*, AMNH 48695, 103 mm; (B) *Odontobutis obscura*, AMS I.27277-001, 68 mm; C) *Odontobutis obscura*, USNM 86108, 115 mm; D) *Ophiocara porocephala*, AMS I.22709-010, 44 mm. Scale bars indicate 0.5 mm.

ceratohyal (Fig. 6A). Other gobioids are more specialized in having the penultimate ray articulate with the anterior ceratohyal (Fig. 6B). In some odontobutids and eleotridines the penultimate ray is relatively close to the anterior/posterior ceratohyal junction, and may lie between ceratohyals; this is most extreme in free-swimming genera such as *Micropercops* and *Hypseleotris,* where the anterior and posterior ceratohyals are relatively widely separated by an undifferentiated cartilage block (Fig. 6C).

Head Canals and Lateral Line. —A lateral line on the body is present only in *Rhyacichthys* (character 9).

In gobioids with developed head canals there is a canal, variously referred to as the lateral canal or oculoscapular canal, extending from the eye to above the preoperculum or operculum (Akihito, 1986). Another canal, referred to as the supraorbital canal, or as part of the oculoscapular canal, runs from just behind the eye forward to above the eyes and towards or to the nostrils. Only in *Rhyacichthys* does the preopercular-mandibular canal connect to the oculoscapular canal and extend onto the mandibular region (character 10). Both of these features are regarded as plesiomorphic. The infraorbital canal extends below the eye only in *Rhyacichthys* and the gobiine *Lophiogobius* (character 11). The canal is not associated with infraorbital bones, but extends ventrally over the cheek in these two genera. In odontobutids, butines, and eleotridines the supraorbital canals are separate, but may be connected by a tube to a single posterior interorbital pore. In many gobiines the canals fuse between the eyes. Because of its uniformity in the primitive gobioids, the separation of the supraorbital canal was not used in the analysis.

Urohyal (character 12). —The ventral transverse shelf on the urohyal reported by Akihito (1986) was found in *Rhyacichthys* and all genera of Odontobutidae, Butinae, and Eleotridinae examined, except for the eleotridines *Leptophilypnus, Microphilypnus, Grahamichthys,* and *Thalasseleotris.* The ventral shelf is absent in other gobioids.

The absence of the shelf in the four eleotridine genera could be interpreted as evidence for this assemblage forming a sister group or series of sister groups to the Gobiinae. However, as discussed below, other characters do not support that conclusion.

Interneural Gap (character 13). —In most odontobutids, butines, and eleotridines the first pterygiophore of the second dorsal fin begins immediately behind the last pterygiophore of the first dorsal fin and there is no interneural space without a pterygiophore (Fig. 7A). In *Rhyacichthys* there is a gap, but the serially and secondarily associated pterygiophores of the spine in the second dorsal fin are closely applied to each and occupy the same interneural space, a condition not found in other gobioid fishes; it is probable that the last (secondarily associated) pterygiophore of the second dorsal-fin spine of *Rhyacichthys* has shifted forward. In butine genera with 10 precaudal vertebrae the first two anal pterygiophores align with the fourth pterygiophore of the second dorsal fin. In gobiines, xenisthmids, and some eleotridines there is an interneural space between the two dorsal fins without a pterygiophore (Fig. 7B). In these groups the first two anal pterygiophores line up with the third pterygiophore of the second dorsal fin. Evidence suggests that the development of the gap in these groups may represent a specialization by displacement of the second dorsal fin posteriorly. If the condition in *Rhyacichthys* is plesiomorphic and homologous with the interneural gap of other gobioids, then the absence of an interneural gap would define the butines
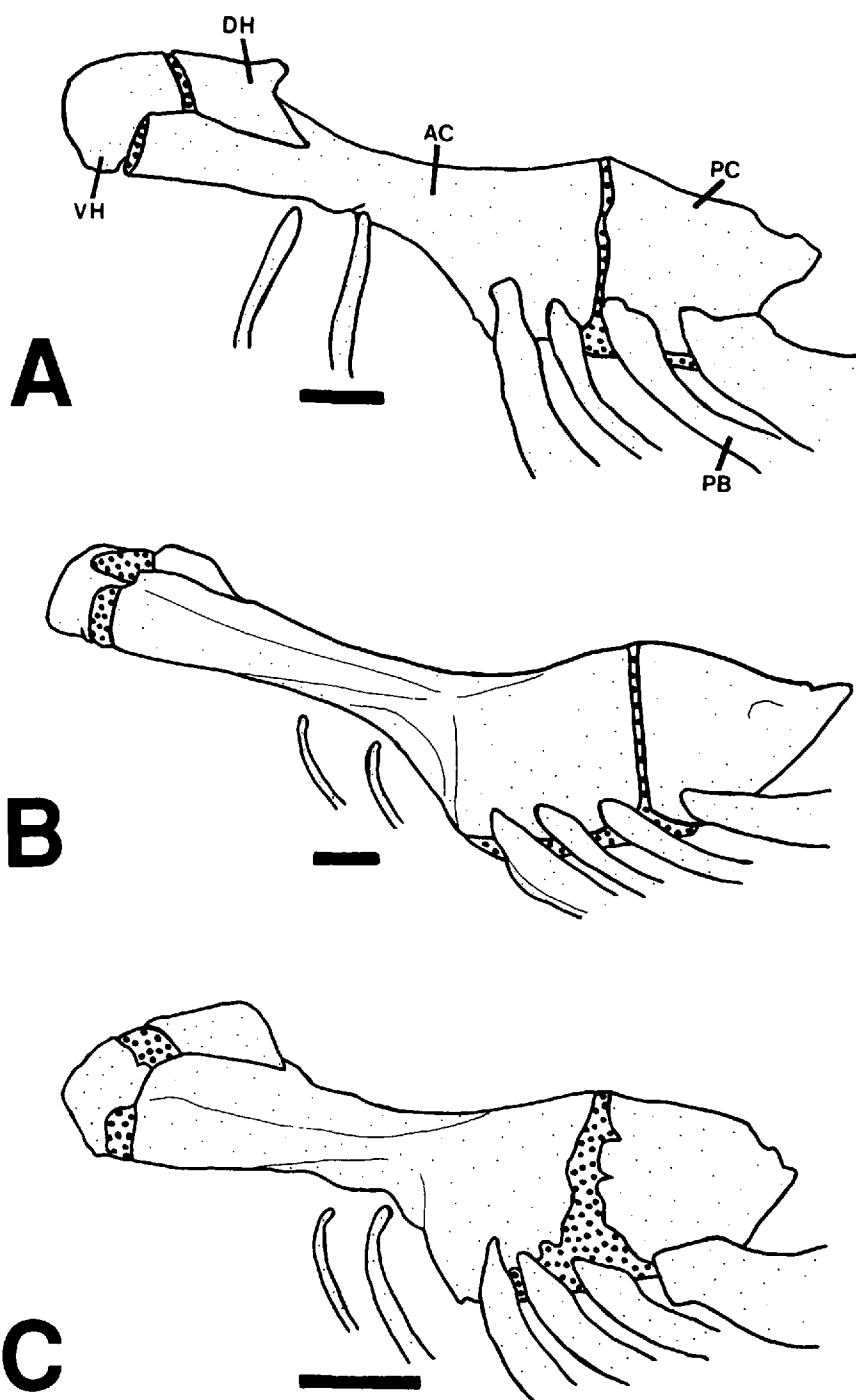
Figure 6. Lateral views of hyoid bar showing position of penultimate branchiostegal ray of: A) *Rhyacichthys aspro,* AMNH 48695, 103 mm; B) *Bunaka gyrinoides,* AMS I.31519-001, 74 mm (right side, reversed); C) *Micropercops swinhonis,* AMS I.27275-002, 42 mm (right side, reversed). Abbreviations: AC—anterior ceratohyal; DH—dorsal hypohyal; PB—penultimate branchiostegal ray; PC—posterior ceratohyal; and VH—ventral hypohyal. Scale bars indicate 1 mm.
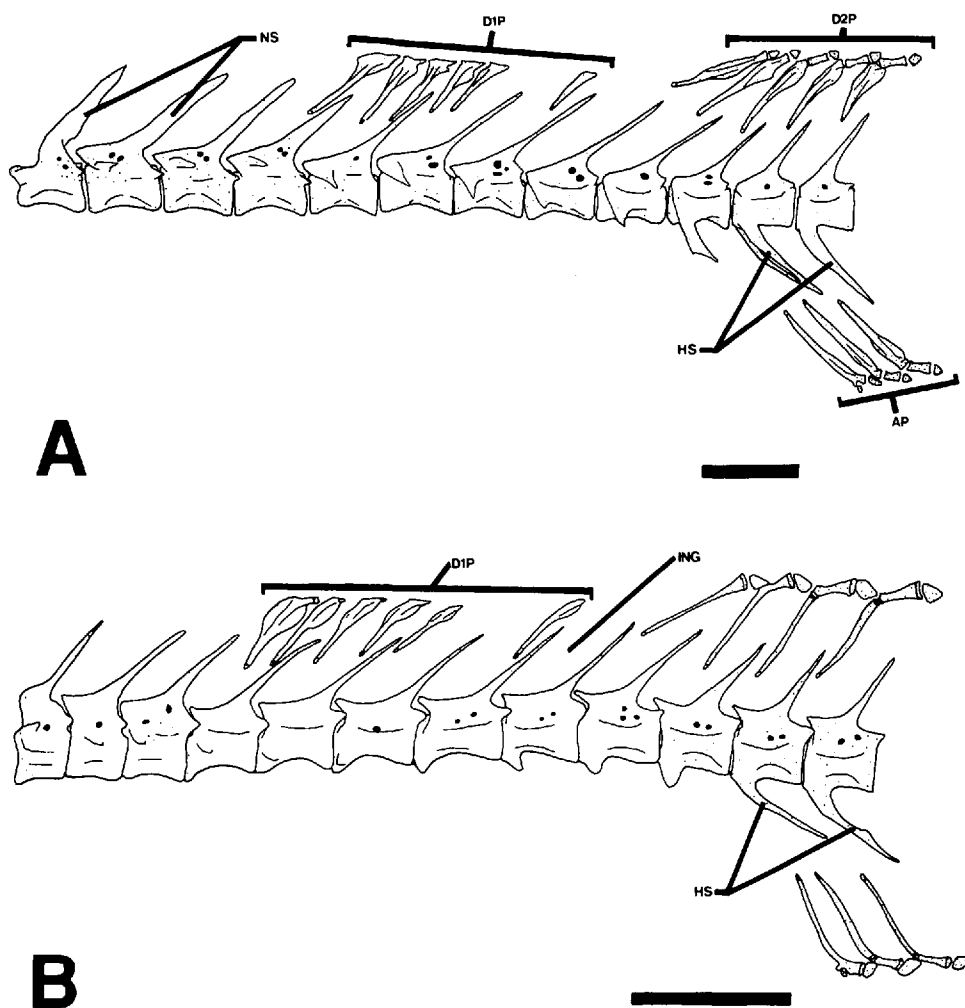
Figure 7. Precaudal vertebrae and first two caudal vertebrae (fin rays and ribs omitted) of: A) *Eleotris melanosoma,* AMS I.22709-009, 44 mm, showing 3(1221) arrangement of first dorsal-fin pterygiophores and no interneural gap; B) Xenisthmidae, new gen. and sp., AMS I.32484-001, 31 mm, showing 3(2211) arrangement of first dorsal-fin pterygiophores and an interneural gap. Abbreviations: AP— anal-fin pterygiophores; D1P—first dorsal-fin pterygiophores; D2P—second dorsal-fin pterygiophores; HS—anterior two hemal spines; ING—interneural gap; NS—anterior two neural spines. Scale bars indicate 2 mm.

+ odontobutids; other characters do not support that conclusion. In some eleotridines, such as *Ophieleotris,* only the first pterygiophore of the second dorsal fin may be displaced posteriorly, resulting in a gap and two pterygiophores in the following interneural space, a condition not homologous with gobiines. In *Gobiomorphus, Philypnodon* and *Microphilypnus* there is an interneural gap. All have 12 precaudal vertebrae, and the first anal pterygiophore occurs below the fourth or fifth second-dorsal pterygiophore, and 4 or 5 pterygiophores usually precede the first hemal spine. The broad parapophyses in these genera suggest that one or two precaudal vertebrae have been added, resulting in a posterior displacement of the second dorsal fin, but not the anal fin. Consequently the condition may not

Table 1.   Head pore patterns in Odontobutidae, Butinae and Eleotridinae (OC = number of pores in oculoscapular canal, POP = number of pores in preopercular canal)

Genus	OC	POP	Genus	OC	POP
Odontobutidae			Eleotridinae		
Micropercops	3, 12	2–4	*Belobranchus*	0	0
Odontobutis	0, 2–6	0, 2–4	*Bunaka*	0	0
Perccottus	0, 12	0, 5	*Calumia*	0	0
			Dormitator	0	0, 2–3
Butinae			*Eleotris*	0	0
Bostrychus	12	5	*Erotelis*	0	0
Butis	12	5	*Gobiomorphus*	0–5	0, 2–4
Hannoichthys	12	5	*Gobiomorus*	5	3–4
Incara	12	5	*Grahamichthys*	0	0
Kribia	0	0	*Guavina*	0	3–4
Milyeringa	0	0	*Hemieleotris*	3	3–4
Odonteleotris	12	5	*Hypseleotris*	0, 3–5	0, 2–4
Ophiocara	11	5	*Kimberleyeleotris*	0	0
Oxyeleotris	12	5	*Leptophilypnus*	5	2–3
O. (Dwarf)	0	0, 2	*Microphilypnus*	0	0
Parviparma	10–12	4	*Mogurnda*	0	0
Pogoneleotris	12	5	*Ophieleotris*	0	2
Prionobutis	12	5	*Philypnodon*	0	0
Typhleotris	0	0	*Ratsirakea*	0	0
			Tateurndina	0	0

be homologous with the condition found in gobiines and xenisthmids. However in *Grahamichthys, Leptophilypnus,* and *Thalasseleotris* there are 10 precaudal vertebrae and the gap is structurally identical to the condition found in gobiids and xenisthmids. A gap also occurs in some species of *Mogurnda,* which have 13–15 precaudal vertebrae and 7–10 dorsal spines. Consequently it is not known whether the gap results from fin displacement or loss of a pterygiophore. A gap also occurs in *Oxyeleotris nullipora,* and in some specimens of *Ratsirakea,* which is highly variable in the pterygiophore formula with the gap sometimes occurring before the last pterygiophore of the first dorsal fin. A gap structurally comparable to gobiines also occurs in xenisthmids. It is suspected that the gap has evolved repeatedly in gobioid fishes. Although clearly a specialization, interpretation of homology is difficult. The character was included, because it was the primary feature that suggested that some eleotridine genera might represent the sister group to gobiines.

Head Pores. —The positions of head pores and their numbers have been used extensively in defining genera and species of gobioid fishes. The terminology for the pores varies considerably. Homologies based on pore position are unclear, because the development of pores has not been well studied. Pores may develop at the junction of fusion of the canal segments, or develop as a perforation or branch in the canal.

In *Rhyacichthys* the various head canals are continuous without breaks and involve 32 pores (Miller, 1973), 12 on the oculoscapular canal, 9 on preopercular mandibular canal, and 11 on the infraorbital canal. The most complete head pore development in primitive gobioid fishes, other than *Rhyacichthys,* involves 17 pores (5 on preopercular canal and 12 on oculoscapular canal), all paired on each side of the head, except for in the posterior interorbital region, where there may be a single median pore. The reduction from 32 pores in *Rhyacichthys* involves loss of 11 pores from the infraorbital canal and 4 from the preopercular-man-

dibular canal. Further reduction in number of pores in odontobutids, butines, and eleotrines is usually associated with reduction of the canals, but sometimes may be related to pore loss from a canal (Akihito, 1986).

Head canal development in odontobutids is variable. Some species have extensive canal development, others have partial development of canals (which are reduced to short segments), and others lack canals (Table 1). In most species of *Perccottus* all pores are absent, but *Perccottus chalmersi* has extensive canal development, with 17 pores. Similarly, in *Micropercops* some species have 17 pores, but others have 2–4 preopercular pores and sometimes a short tube with a pore at each end over the operculum and the supraorbital canal is short extending from immediately behind the eye to above the front half of the eye with 4–6 pores. In *Odontobutis,* canals may be absent or reduced to 1 or 2 short separate segments on preopercular margin and 1–3 detached segments on supraorbital canal. The canal and pore patterns vary slightly with species and subspecies (Iwata et al., 1985).

Akihito (1971) reported extrascapulae absent in *Odontobutis.* It is not present in a single specimen of *Micropercops* we examined, but they would be expected in *Perccottus chalmersi* based on pore pattern. Extrascapulae also occur in *Rhyacichthys,* most butines, and the xenisthmid genus *Xenisthmus.*

Butines generally have 17 pores (Table 1). Pores are absent only in *Oxyeleotris nullipora* Roberts, and the blind *Typhleotris* and *Milyeringa,* and species of *Kribia* (all of which are small, less than 30 mm SL), or reduced to two preopercular pores in the dwarf species *Oxyeleotris paucipora.* In some species of *Bostrychus* and *Oxyeleotris* 1–3 pores may be lost.

In eleotridines pores are absent in most genera, or reduced in comparison with most butines (maximum of 9 in species studied). Pores are best developed in *Gobiomorus* and *Leptophilypnus.* In some genera only 2–4 preopercular pores are present. Others have interorbital and infraorbital pores. Other species of *Gobiomorus* apparently have more numerous pores (P. Wongrat, in litt.). Consequently, we conclude that the reduction of pores in the eleotridines is a specialization that occurs within the group, rather than representing a specialization defining the subfamily.

Head pore numbers were not used in the final analysis due to the high variation within some genera.

Sensory Papilla Pattern. —In general, taxonomic studies have indicated that the pattern of papillae is often consistent within a species or genus. Some genera have been defined primarily on the basis of the papilla pattern. Hoese (1983) noted that there are typically two basic papilla patterns recognized in gobioid fishes: transverse and longitudinal (Fig. 8). Hoese (1983) suggested that the orientation of papillae was as important as the arrangement of papillae. Under high magnification it can be seen that papillae are usually oval, rather than round. Hoese (1983) suggested terminology to take the orientation of the papillae with respect to the papillary line into account. Both the longitudinal and transverse patterns have two cheek lines in common: an upper horizontal line (starting below the eye, usually called row b) and a lower horizontal line (starting at the upper jaw, usually called row d) with the papillae at right angles to the axes of the lines. In the transverse pattern there are four or more vertical rows of papillae on the cheek, with the papillae axes at a right angle to the axis of the row. In the longitudinal pattern there are three or four additional longitudinal lines between the upper and lower lines (b and d) with the papillae axes along the axis of each line.

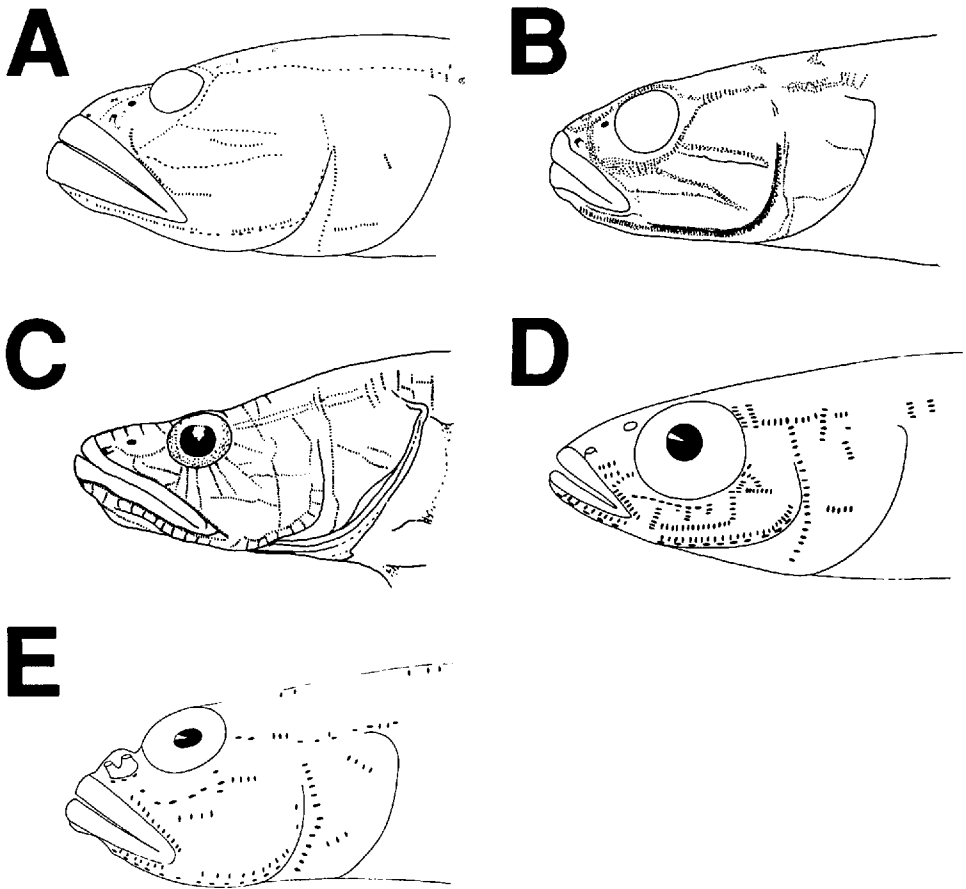Our study shows that the papillary patterns do show some correlation with

Figure 8.   Sensory papillae patterns in eleotridid fishes: A) Longitudinal pattern based on *Odontobutis obscura*, NTM S.11697-001; B) Multiple longitudinal pattern based on *Mogurnda* sp., USNM 210768; C) Transverse pattern, based on *Philypnodon grandiceps*, based on several specimens, AMS; D) Mixed pattern, based on *Kimberleyeleotris hutchinsi*, based on type material, WAM 25684; E) Reduced transverse pattern based on *Thalasseleotris adela*, AMS I.18241-035.

other characters. The patterns are most consistent within groups believed to be primitive, with much less consistency within the derived group (Eleotridinae). In the odontobutids the pattern is longitudinal in all three genera (Fig. 8A). All butines except *Pogoneleotris* have a transverse pattern (Table 2). In some genera many of the vertical lines are absent (reduced transverse pattern).

In the eleotridines, several patterns are recognized: a simple longitudinal pattern with each line composed of a single row of papillae (as in *Odontobutis*, Fig. 8A); a multiple longitudinal pattern (Fig. 8B), with one or more longitudinal lines composed of multiple rows of papillae, a transverse pattern (Fig. 8C), a mixed pattern, with both longitudinal and vertical lines (Fig. 8D), and a reduced transverse pattern, with most of the vertical rows reduced or absent (Fig. 8E). Two patterns often occur in the same genus (Table 2). There is no one pattern that could be said to be typical of the eleotridines.

We did not use the papillary patterns in the analysis of relationships because of polarity problems, but include the data here to show that classifications based

Table 2. Papillae and pterygiophophore patterns in Odontobutidae, Butinae and Eleotridinae (L = longitudinal pattern, ML = multiple longitudinal, T = transverse pattern, RT = reduced transverse, MX = mixed longitudinal and transverse)

Genus	Papilla pattern	Pterygiophore formula	Genus	Papilla pattern	Pterygiophore formula
Odontobutidae			Eleotridinae		
Micropercops	L	variable	*Belobranchus*	MX	3(1221)
Odontobutis	L	variable	*Bunaka*	L	3(1221)
Perccottus	L	variable	*Calumia*	RT	3(1221)
			Dormitator	L	3(12211)
Butinae			*Eleotris*	T	3(1221)
Bostrychus	T	3(2211 . . .)	*Erotelis*	T	3(1221)
Butis	T	3(2211)	*Gobiomorphus*	L	variable
Hannoichthys	T	3(2211)	*Gobiomorus*	L	3(2211)
Incara	T	3(2211)			
Kribia	T	3(1221)	*Grahamichthys*	L?	3(2211)
Milyeringa	RT	4(212)	*Guavina*	MX	3(12211)
		4(221)	*Hemieleotris*	L	3(2211)
Odonteleotris	T	unknown	*Hypseleotris*	L, ML	3(1221)
Ophiocara	T	3(2211)			3(2211)
Oxyeleotris	T	3(2211)	*Kimberleyeleotris*	T	3(12210)
Parviparma	T	4(3211)			3(12211)
Pogoneleotris	L?	unknown	*Leptophilypnus*	T	3(12210)
Prionobutis	RT	3(2211)	*Microphilypnus*	T	3(22110)
Typhleotris	T	3(2211)	*Mogurnda*	ML, MX	variable
			Ophieleotris	L	3(1221)
					4(321)
					4(2310)
			Philypnodon	T	3(122110)
			Ratsirakea	L, MX	3(1221)
			Tateurndina	L	variable
			Thalasseleotris	RT	3(22110)

primarily on the papillary pattern will result in a classification radically different from the one presented here.

First Dorsal-fin Pterygiophore Formula. — The pterygiophore formula was first used by Birdsong (1975). The formula was later modified and considerable data were provided by Birdsong et al. (1988). The prime difficulty with the character is that it has not been polarized. Two patterns in the arrangement of the first 5 pterygiophores are common in gobioids. In most there are 3 neural spines preceding the first pterygiophore (4 or more in some). The formula expresses this number followed by the arrangement with respect to the interneural spaces. In one pattern [3(221 . . .)] there are 3 neural spines without preceding pterygiophores, then two pterygiophores in the next interneural space, then 2, then 1 (Fig. 7B). Following these five there are one to five additional pterygiophores spaced 1 per interneural space. The second pattern (Fig. 7A) has the pterygiophores arranged 3(122 . . .). Other patterns exist 3(121 . . .), 3(212 . . .) or 4(321), etc., and many of these occur in genera referred to here as variable. Those genera with a variable pattern usually have more than one pattern occurring in a single species.

The pterygiophore pattern shows a high degree of correlation with the papilla pattern in the butines (Table 2). In odontobutids, the pterygiophore pattern is highly variable within a species. In *Rhyacichthys* and butines, all except *Kribia* have the first five pterygiophores arranged as 3(221). As for the papilla pattern, the pterygiophore pattern is not consistent within the eleotridines and can vary

within a genus (Table 2). For example, two patterns occur in *Hypseleotris* [3(1221) or 3(2211)], depending on the species. Both patterns also occur in gobiines.

We did not include this character is our analysis because of its high variability in some genera and uncertainty over polarization. Even if the condition in *Rhyacichthys* is accepted as the primitive condition, the character would not be informative for major groupings.

CLASSIFICATION OF TAXA PREVIOUSLY ASSIGNED TO THE ELEOTRIDIDAE

Odontobutidae new family

The diagnosis presented here is based primarily on *Odontobutis* and *Micropercops,* because cleared and stained specimens of the only other genus in the family, *Perccottus,* were not available. The family is characterized by the following: infraorbital bones usually present; sclerotic bones usually present (one specimen of *Micropercops* has two sclerotics in one eye and one in the other); scapula large, excluding proximal radial from contact with cleithrum; middle radial of first pterygiophore of second dorsal fin autogenous (absent of fused to proximal element in some specimens of *Micropercops*); dorsal procurrent caudal cartilage small, not expanded anteriorly to support anterior unsegmented caudal-fin rays, and not expanded posteriorly over distal tip of anterior epural; papillae arranged in longitudinal pattern; pterygiophore formula of first dorsal fin variable; at least some body scales with one or more basal rows of distally truncated (transforming) cteni. A summary of features is shown in Table 3.

We are unable to provide evidence for the monophyly of this group, mainly due to our limited knowledge of an immediate outgroup to gobioid fishes. We also have not studied the osteology of *Perccottus*. Based on phenetic similarities in numbers of vertebrae and first dorsal-fin pterygiophores, Birdsong et al. (1988) placed *Micropercops* and *Perccottus* in their *Micropercops* group. They did not assign *Odontobutis* to a group even though its vertebral and first dorsal-fin pterygiophore numbers are identical to the *Micropercops* group. Three plesiomorphic characters (scapula large, excluding upper proximal radial from contact with cleithrum; presence of one or more rows of transforming cteni on body scales; and lack of anterior expansion of the procurrent caudal cartilages) are otherwise known only from the Rhyacichthyidae (*Acanthogobius* also has transforming cteni, but we argue that this is most parsimoniously interpreted as a reversal). The presence of the derived conditions for these characters in the remaining gobioids is evidence for their monophyly. An additional potential synapomorphy linking all gobioids except *Rhyacichthys* and odontobutids is the loss of the arrector ventralis muscle, which normally attaches to the median half of the dorsalmost pectoral-fin ray (Grenholm, 1923; Gosline, 1980). This muscle is well developed in *Odontobutis* and *Micropercops* (*Perccottus* has not been surveyed) and weakly developed in *Rhyacichthys*; it appears to be absent in other gobioids, but has not been adequately surveyed. A more detailed survey of this character is currently in progress by the junior author and R. D. Mooi. This character was brought to our attention by G. D. Johnson, who further suggested that the loss of the arrector ventralis may be associated with the loss of the dorsalmost pectoral-fin ray (see Johnson and Brothers, 1993, for further discussion).

Odontobutids are confined to freshwaters of the northwest Pacific, from China, Korea, Japan, Russia and northern Vietnam (Iwata et al., 1985, in part). Currently only about four or five species are recognized.

Table 3. Character states used in classification. 1) adductor mandibulae tendon, 2) anterior procurrent cartilage, 3) posterior procurrent caudal cartilage, 4) scapula/radial position, 5) second dorsal radial, 6) bony preopercular canal support, 7) scale cteni, 8) penultimate branchiostegal ray position, 9) lateral line, 10) preopercular mandibular canal, 11) infraorbital canal, 12) urohyal shelf, 13) interneural gap, 14) interhyal position, 15) branchiostegal ray number, 16) pelvic fin structure

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Rhyacichthyidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontobutidae	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0
Butinae	0	1	0	1	1	0	1	1	1	1	1	0	0	1	0	0
Kribia	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	0
O. aruensis/nullipora	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	0
Eleotridinae	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0
Tateurndina	1	1	?	1	1	1	1	1	1	1	1	0	0	1	0	0
Grahamichthys/Thalasseleotris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Microphilypnus/Leptophilypnus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Gobiinae	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1

Family Gobiidae

Provisionally we regard the remaining groups studied as belonging to a single family, but we do not attempt placement here of Xenisthmidae, Microdesmidae and Kraemeriidae. The family is defined by the following specializations: no autogenous middle radial in first pterygiophore of second dorsal fin; upper proximal radial of pectoral fin usually in contact with cleithrum, extending well above scapula; anterior elongation of the procurrent caudal cartilage; and scales without transforming cteni. Two (Butinae and Eleotridinae) of the three subfamilies were previously grouped as a separate family or as a subfamily of the Gobiidae. The subfamily Gobiinae was diagnosed previously (Hoese, 1984) as a distinct family.

BUTINAE Bleeker. We are unable, at present, to provide apomorphies defining the group. We recognize the group because there are apomorphies defining the two other gobiid subfamilies. We recognize that the group may be paraphyletic. The subfamily is characterized by the following primitive features: adductor mandibulae tendon from A1-beta segment attaches to a process anteriorly on the maxilla; usually 17 segmented caudal rays; upper cartilage plate elongate anteriorly, but not expanded posteriorly over the tip of the epural or epurals; head pores usually well developed (with an anterior nasal pore and supratemporal canal pore usually present; pores reduced or absent only in the dwarf species Kribia spp., Oxyeleotris nullipora and O. paucipora, and the blind cave genera Milyeringa and Typhleotris); bony preopercular canal support usually extends full length of preopercular bone; extrascapulae and nasal bones usually present. A summary of all features studied is given in Table 3.

Other features include: sensory papilla pattern transverse or reduced transverse (with possible exception of Pogoneleotris); pterygiophore formula 3(2211) or 3(22111) (except in Kribia which has 3(1221)). The infraorbital and sclerotic persist only in some species of Bostrychus and Oxyeleotris.

The Butinae comprises 13 genera confined to freshwater and estuaries of the tropical Indo-Pacific and West Africa (Table 1). These genera were either placed by Birdsong et al. (1988) in their Butis group (in part) or Dormitator group (in part), or were unplaced (Parviparma Herre, Incara Rao and Pogoneleotris). Monophyly of included genera remains to be evaluated.

ELEOTRIDINAE Gill. The subfamily is characterized by the following specializa-

tions in relation to the Butinae: adductor mandibulae tendon from A1-beta segment attaches directly to the maxilla, without any process, usually below the attachment of the maxillodentary ligament; usually 15 segmented caudal rays (uppermost and lowermost segmented ray lost or failing to become unsegmented); upper cartilage plate expanded anteriorly and posteriorly, with a short projection extending over the tip of the epural(s); head pores poorly developed, nasal canal segment and lateral canal segment above preoperculum absent (no nasal or supratemporal pores, extrascapulae absent, nasal bones often present, but absent in some genera); bony canal preopercular canal support confined to the vertical portion of the preopercular bone; infraorbital (other than lacrymal) and sclerotic absent.

Information provided by P. Wongrat suggests that the nasal section and lateral canal section behind the eye may be present, but reduced in *Gobiomorus.* We did not find this to be the case in *Gobiomorus maculatus,* but did not examine other species. If the canals are more fully developed in other species of *Gobiomorus,* the reduction of head pores does not constitute a character defining the group.

The patterns of sensory papillae and pterygiophores of the first dorsal fin are highly variable and sometimes differ between species in the same genus.

The two main characters distinguishing this group (tendon and caudal skeleton) were first noted by Akihito and Meguro (1974) as a basis of separating *Ophiocara* and *Ophieleotris,* which had previously been considered as congeneric. Although the butine genus *Kribia* has 14 or 15 segmented caudal rays, evidence given above indicates homoplasy in the reduction from the primitive segmented caudal ray condition.

The Eleotridinae include 21 or 22 genera (Table 1). These were variously placed by Birdsong et al. (1988) in their *Butis* group (in part), *Dormitator* group (in part), *Eleotris* group, *Gobiomorphus* group, or *Hypseleotris* group, or were unplaced (*Leptophilypnus, Microphilypnus,* and *Tateurndina*). A more detailed phylogeny of this Eleotridinae will be presented elsewhere.

The subfamily occurs worldwide in tropical and temperate regions. Most genera are confined to freshwater or mangrove environments. The group appears to have its greatest number of species in the New Guinea-Australia-New Zealand region and in the New World, but the high numbers for those regions may reflect better knowledge of those faunas.

DISCUSSION

The cladogram upon which the classification above is based is shown in Figure 9. Character states are shown in Table 3. Only the major groups are shown in the cladogram. From the characters examined we were unable to define the Odontobutidae or the Butinae. The family Rhyacichthyidae forms the sister group to the remaining gobioids, which are separated by 5 characters from rhyacichthyids. The family Odontobutidae forms the next sister group to the remaining gobioids, which are separated by 4 characters from odontobutids. The three remaining groups form an unresolved trichotomy. The eleotridines are defined by two characters and the gobiines by two characters. Hoese (1984) listed a third specialization for the gobiines, based on the orientation and articulation of the palatines and ethmoids. Too few characters are included to allow resolution of genera within the Butinae and Eleotridinae. Inclusion of all genera listed in Table 3 resulted in two trees, which differ only in placement of *Tateurndina,* because of the uncertainty of the character state of the procurrent caudal cartilages. Three groups (*Kribia* spp., *Oxyeleotris aruensis,* and *O. nullipora*) form a sister group to the
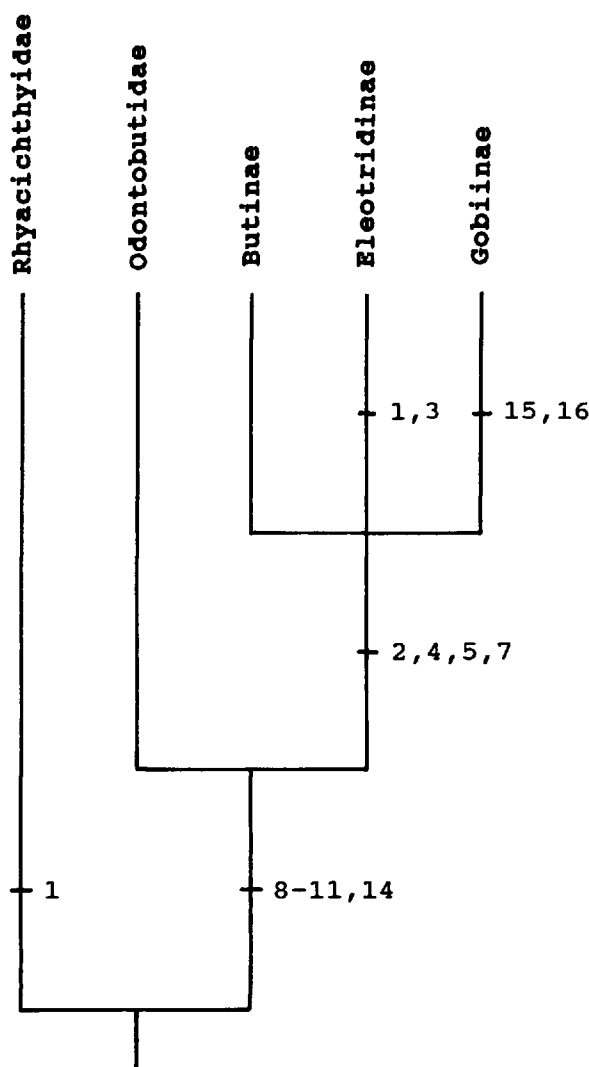
Figure 9. Hypothesized interrelationships of Rhyacichthyidae, Odontobutidae, and the gobiid sub-families Butinae, Eleotridinae and Gobiinae. Character numbers are clarified in Table 3 and in the text.

eleotridines, based on the reduction of the bony support of the preopercular canal. Because the bony canal support is also reduced in most gobiines and the support is not reduced in other species of *Oxyeleotris,* we do not believe the character is sufficient to place these taxa with the eleotridines.

In many cases characters that traditionally have been used involve loss of structures that are already relatively reduced or rudimentary in gobioid fishes. For example, the dorsal postcleithrum, infraorbital and mesopterygoid are ru-dimentary and apparently lost repeatedly, often being absent only in some species of a particular genus. Where we found evidence for convergence or reversals, the species involved are almost always of small size. Examples include the following species: *Kribia* spp., *Oxyeleotris nullipora, Thalasseleotris adela,* and *Tateurndina*

ocellicauda, all species less than 40 mm SL as adults. Losses and reduction in these taxa may be the result of paedomorphosis. Some of these species have also lost a number of primitive features, such as lack of ossification of scapula, that also appear to be lost independently within gobiines. Evidence for reversal and some convergence (such as reduction of segmented caudal ray number in *Kribia*) was supported by structural features indicating lack of homology of apparently similar characters. For these reasons, we have relied heavily, in defining the Eleotridinae, on characters that involve innovations, rather than only relying on structural losses. We did find evidence of high congruence of papilla pattern (in odontobutids and butines) and pterygiophore pattern (butines), but not within the Eleotridinae, and do not regard those characters as informative, other than possibly providing information of the primitive character states within those groups.

Although not studied in detail, the characters examined suggest that the family Xenisthmidae groups with the butines. That problem is currently under study by one of us (A.C.G.). Placement of the remaining gobioids is also ambiguous. The family Kraemeriidae groups with the gobiines. Microdesmidae are characterized by several specializations, some of which occur in some eleotridine genera. At least some, if not all, ptereleotrines (primitive microdesmids) have the procurrent cartilage extending over the tip of the epural. The element associated with the epural is segmented and not displaced dorsally, a condition slightly different from that of eleotridines. The adductor mandibulae tendon attaches to the middle of the maxilla, as in eleotridines. Ptereleotrines have 5 branchiostegal rays and an interneural gap, characteristic of gobiines. However, they also have a single pterygiophore preceding the first hemal spine, with the second anal pterygiophore articulating with the posterior tip of the hemal spine. This character also occurs in the eleotridine genera *Grahamichthys* and *Thalasseleotris.* Consequently present evidence suggests that the microdesmids might form a subgroup of the eleotridines, with *Grahamichthys* and *Thalasseleotris* possibly forming the sister group of the group currently referred to as the microdesmids.

ACKNOWLEDGMENTS

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